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The effect on feeding and wheel running behaviours of housing rats in pairs

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By

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Abstract

The effects on feeding of moving animals from individual- to pair-housing were explored in the present three experiments. Wheel access is known to result in a temporary suppression of feeding. The move to pair-housing was compared with the effect of wheel access. In Experiment 1, a group of rats was moved from individual to pair-housing (IP group) and compared to a group of individually-housed rats (IND group) and a group of chronically pair-housed rats (PAIR group). The animals in the IP group showed a temporary (three days) suppression in feeding (initially 23%). When half of the IND and PAIR group animals were moved between individual- and pair-housing on alternate days (IND-ALT and PAIR-ALT groups, respectively) (Experiment 2), only the rats in the IND-ALT group showed a three day feeding suppression (initially 40%). Experiment 3 examined the effect of the simultaneous introduction of wheels and transfer of housing conditions. The feeding suppression induced by the transfer from individual- to pair-housing was evident prior to, and of a shorter duration than, the feeding suppression induced by wheel access. These results indicate that the feeding suppression, induced by a housing shift, is not the same as that evident when rats are given wheel access. It is concluded that the stress associated with novel pair-housing was responsible for the decrease in feeding. Novelty does not appear to account for the suppression of feeding following wheel access.

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Table of Contents

The Effect On Feeding and Wheel Running Behaviours of Housing Rats In Pairs

In animal studies, a negative relationship between energy expenditure and caloric consumption has been reported when there is a shift from a sedentary to a more active state. When a running wheel is introduced into a rat's cage, there is a decrease in the animal's caloric consumption lasting about seven to ten days (e.g., Bauman, 1992; Collier, 1970; Collier, Hirsch & Leshner, 1972; Jennings & McCutcheon, 1974; Levitsky, 1970; Looy & Eikelboom, 1989; Premack & Premack, 1963; Tokuyama, Saito & Okuda, 1982). The present investigation determined if this change in rats' feeding behaviour is unique to running wheel access or could be induced by another significant change in the environment; moving animals from individual- to pair-housing. If the effect is non-specific, then other means of changing the environment should result in similar decreases in caloric consumption.

Running Wheel Access and Feeding

Several studies have shown that when wheels are introduced, rats change their eating behaviour (Bauman, 1992; Collier, 1970; Jennings & McCutcheon, 1974; Levitsky, 1970; Looy & Eikelboom, 1989; Premack & Premack, 1963; Tokuyama, et al.., 1982). Looy and Eikelboom (1989) found that male rats with ad-lib access to food and water decreased their food consumption by about 37 percent when running wheels were made available. However, this decrease was only temporary as by the fourteenth day of wheel exposure, the caloric intake of the active rats had increased and plateaued at a level similar to that of the inactive rats. A longer suppression in feeding, with the presence of running wheels, can be maintained if wheels are only available on alternate days. Mueller, Loft, and Eikelboom (in press), report that for the duration of their study (16 days of wheel access, alternating with days without wheel access), rats continued to show a suppression in feeding each time the wheels were present.

The relationship between wheel running and eating behaviours has been further explored in a series of studies where there is either a period of starvation or where food access is restricted to a short period each day (Campbell & Lynch, 1968; Collier, Hirsch & Leshner, 1972; Hall & Hanford, 1954; Hall, Smith, Schnitzer & Hanford, 1953; Kanarek & Collier, 1983; Reid & Finger, 1955; Routtenberg, 1968; Routtenberg & Kuznesof, 1967; Scalfani & Rendel, 1978; Stevenson & Rixon, 1957). With wheel access, rats that are food deprived show elevated running, compared to ad-lib fed rats. With food-deprived rats, those with wheel access eat less during food availability than those with no wheel access. The combination of reduced food intake and increased running can prove fatal in about 7 to 14 days. The suppression of feeding when animals can run is so strong that even when the animal is food deprived, wheel access reduces consumption further.

Is the Change in Feeding Specific to the Wheel?

It is unclear whether the change in rats' feeding behaviour is specific to the running wheel or some more general, non-specific effect. If the effect on feeding is specific to rats running in the wheels then it would be expected that other modifications of the rats' environment would not result in a suppression of feeding.

There is a literature suggesting a physiological basis for the relationship observed between wheel running and feeding. These studies suggest running results in some physiological change, such as an elevation in body temperature (Paré, 1977) or a change in blood hormones or energy that in turn causes a suppression of feeding (Arnold & Richard, 1987; Broocks, Schweiger & Pirke, 1991; Pirke, Broocks, Wilckens, Marquard & Schweiger, 1993; Richard, Arnold & Leblanc, 1986; Rieg & Aravich, 1992).

Two main physiological-based theories have been proposed to account for the suppression in rats' feeding following running wheel access. The first relates the effects of body temperature on activity and feeding. There is an inverse relationship between temperature and feeding; therefore, with an increase in temperature, ad-lib fed rats show a decrease in feeding (Paré, 1977; Richard, et al., 1986). Since a rat's body temperature would be elevated following wheel running, it follows that feeding will be suppressed. A second theory attributes the decrease in feeding, following activity, to an increase in free fatty acids in the blood (Gollnick, 1967). This results in a temporary feeding suppression until the relationship between the free fatty acid levels and the size of the adipose reserves returns to equilibrium (Collier, 1970). These physiological changes, as a result of wheel access, may explain the suppression of feeding that is observed; however, alternate explanations for wheel induced feeding suppression need to be examined.

Routtenberg (1968) proposed that the decrease in rats' caloric intake, when the wheel is initially introduced, and the recovery of feeding during a prolonged period of wheel access, can be accounted for by the novelty of the wheel. Rats may decrease their intake in response to the novelty of the wheel, and once the novelty is lost, recover their feeding to pre-wheel exposure levels. Routtenberg (1968) supported the novelty hypothesis by demonstrating that even when rats were given access to locked wheels (preventing energy expenditure), they temporarily showed a small suppression in their intake of food. Presumably, the novelty of the wheel, alone, was sufficient to decrease rats' intake of calories.

Premack and Premack (1963) argued that reinforcers may be substituted for each other such that rats may select reinforcers based on what is available. Therefore, since in "normal" cages there is little to do, rats are limited to eating and drinking, they eat in excess. (The level of consumption in these isolated cages may in fact be unhealthy as rats with restricted food access are found to live longer (Sohal & Weindruch, 1996).) However, with environmental enrichment, such as when wheels are made available, the reinforcement derived from running may decrease the need for reinforcement obtained from eating, thus they eat less.

Other situations exist where the addition or removal of a reinforcer has an effect on the remaining or current reinforcers. Exercise has been found to reduce rats' self-administration of psychoactive drugs (Kanarek, Marks-Kaufman, D'Anci & Przypek, 1995; McLachlan, Hay & Coleman, 1994), and the availability of electrical stimulation of the brain results in the suppression of responses to other reinforcers (Frank & Stutz, 1984). This leads to the suggestion that the relationship between wheel running and feeding may not be unique, but may be a general property of the availability of multiple reinforcers.

Pair Housing

If the change in rats' feeding behaviour is not specific to the wheel, but rather a general effect of novelty or environmental enrichment (the addition of an alternate reinforcer), then other changes in the environment, such as pair housing, might produce changes to feeding similar to wheel access; a temporary suppression of feeding. Allowing rats access to another animal has been found to be reinforcing (Evans et al., 1994). If the effect of wheel running on feeding is a result of changes in reinforcement availability or novelty, pair housing should cause a similar suppression in feeding. But, if the effect of wheel access on feeding is specific to running or activity, then pair housing should not produce similar suppressions in feeding.

To date, the day by day effect on feeding of introducing previously individually-housed rats to a pair-housed environment has not been examined extensively. Several studies interested in social facilitation addressed the eating behaviours of animals housed in groups of two or more (Fiala, Snow & Greenough, 1977; Hoyenga & Aeschleman, 1969; Shelley, 1965), but only one study (Hoyenga & Aeschleman, 1969), has assessed the effect on caloric intake of a change from individual- to group-housing of ad-lib fed rats. They moved two individually-housed rats into pair-housing. These two rats did appear to temporarily consume less food than the continually individually-housed rats, but consumption could only be inferred from weight changes as food data were not recorded.

The results of studies that have considered the long-term effect of housing rats in groups of two or more animals per cage on ad lib feeding have been inconsistent.

Experiments by Fiala, et al. (1977) and Shelley (1965) found that over the long term, rats housed individually consumed a significantly greater number of calories per day than rats housed in groups of six or more. Hoyenga and Aeschleman (1969) found, however, at the end of 79 days, that rats housed in groups of four weighed significantly more than individually-housed rats, suggesting that the group housed rats ate more food over a long period. Differences between these studies may be attributed to the sizes of the groups; whereby, overcrowding may have played a role in the results found in Shelley's (1965) study and Fiala et al.'s (1977) study. Hoyenga and Aeschleman (1969) suggest the group housed rats in Shelley's (1965) study may have consumed less food than the individually-housed rats because the food was trampled upon and contaminated with the fecal boll and urine of all the rats in the group condition.

Purpose of Present Studies

The present series of experiments explored the possibility that the initial decrease found in rats' caloric intake when a running wheel is made available is not unique to the wheel, but rather is a non-specific result of environmental enrichment or novelty. Introducing the animals to pair-housing was used as the method of enrichment in the present study. If the rats decreased their intake in response to a shift from individual to pair-housing, then less attention should be given to the specific effect of running wheel activity on feeding and alternate explanations (i.e. novelty, number of reinforcers) should be considered. The first two experiments examined the effect on rats' feeding of moving them from individual to pair-housing. In the third experiment the effect of pair housing on the wheel running-induced feeding suppression was explored. If the wheel induced feeding suppression is non-specific, then suppression is anticipated to be less severe if the animals were already in an enriched environment.

Experiment 1

The first experiment considered the effects on feeding of housing rats either individually or in pairs, and subsequently, the effects of a shift from one to the other. A comparison was made of the feeding behaviours of continually individually-housed rats (IND group), continually pair-housed rats (PAIR group), and rats that were moved from isolation to pair housing (IP group).

One obvious complication in the present studies is that with pair-housing, consumption of individual animals can not be determined. The food data are a measurement of the combined effect of two animals. This has two consequences. First, it is necessary to randomly pair the continually individually-housed animals so that their food data can be combined, thereby equating data for all three groups.

Secondly, in analysing pair-housed animals' feeding data, effects may be due either to a change in consumption of both animals or to a change in only one animal's consumption. For example, a dominant animal might restrict the consumption of the other animal. While this ambiguity with pair-housing can not be explicitly tested, it can be partially addressed by looking at how the weights of individual animals change. By examining each animal's day to day weight change, the feeding behaviours of paired animals can be better understood. If one rat is eating normally while the other is not eating, the first animal should show normal weight gain while the other should show a drastic weight decrease. In this case there should be a large difference in the weight change of the two animals. If both animals eat similar amounts, their weight change should be similar.

Two approaches to pair-housed feeding data follow from this analysis of weight change. To account for an effect of dominance, the variance in weight change in each of the three Housing conditions was examined. If there was a larger consumption difference within pairs from the IP group, then a larger weight change variance would be expected. However, if the difference in feeding behaviours between IP individuals, following the shift to pair-housing, is similar to that of partners/pairs' feeding in the IND and PAIR groups then weight change variance should be similar in all groups. This would suggest that both animals were showing similar consumption in the IP group.

A second check is to co-vary out the difference in the pair's weight change. If the animals moved to pair-housing are both showing a decrease in food intake, then the weight change *difference* should be similar to that of the other groups of rats. However, if food intake in animals moved to pair-housing is suppressed because one animal prevents the other from feeding this should result in a big weight change difference in the paired group relative to the other two groups. Thus the size of the weight change difference would be correlated with the decrease seen in total food consumption. An analysis of co-variance (ANCOVA) co-varying out weight change difference will correct for this type of feeding effect resulting from moving animals to pair-housing.

Method

Subjects. Forty-eighty male Sprague-Dawley rats (180-215 grams) from Charles River Canada were housed, either individually or in pairs, depending on the experimental condition, in polycarbonate shoe-box cages (47.5 x 26.25 x 20 cm) with wire lids that hold food and water bottles.

Throughout the experiment, rats had ad-lib access to Rat Diet (PMI Feeds Inc.) pellets and tap water, and were handled daily. The holding room was maintained on a 12:12 light-dark cycle (lights on between 8:00 am and 8:00 pm) and maintained at a temperature of approximately 21^{0}C.

Procedure. For the first seven days after arrival, all rats were handled and weighed daily. The rats' food and water consumption, and body weights were measured in the morning starting on the eighth day (Day -14 of experiment), after they had adjusted to the colony conditions. The Beta Chip on the bottom of each cage was checked daily so that any food spillage could be excluded from consumption. To ensure that adequate amounts of food and water were available to the rats, the food was topped up with fresh pellets daily (bringing it to approximately 160 grams of food per cage) and water bottles were refreshed daily. Cages and water bottles were cleaned weekly.

Upon arrival, for the purpose of data collection and later housing changes, all rats were randomly assigned to pairs. Initially 16 rats were housed in pairs (PAIR group) and 32 rats were individually housed in polycarbonate shoe-box cages. The PAIR rats and the 16 IND rats remained in their respective living condition for the duration of this experiment. The other 16 rats (the IP group) that were originally individually housed were moved to pair housing 22 days after arrival (Day 0). The cages into which these rats were moved were new to both rats. These rats remained pair housed until Day 8 of the experiment.

Body weight, food intake, and water intake were measured daily (when animals were rehoused) throughout this experiment.

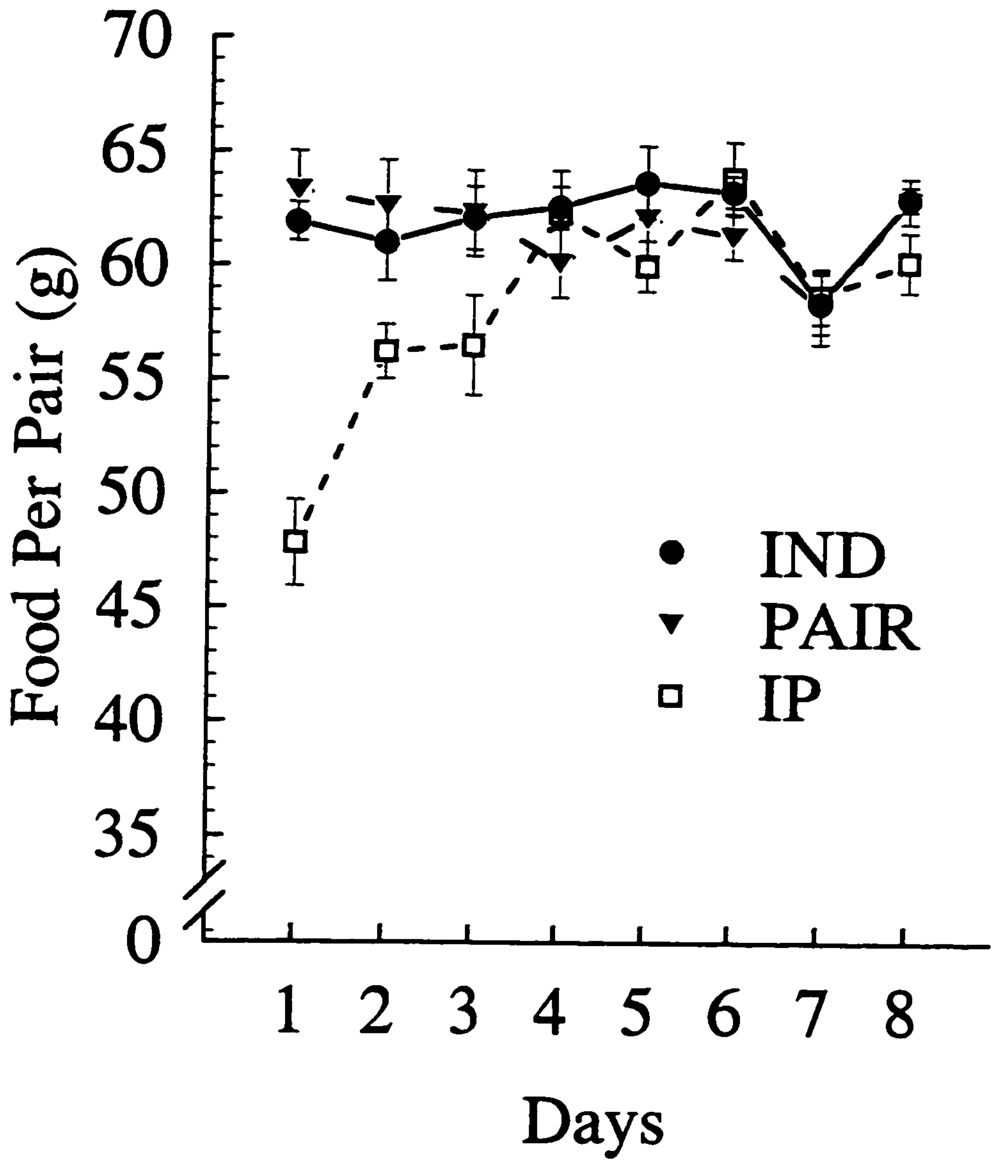
Results

Baseline. The last 4 days of data before moving the animals in the IP group to pair-housing were used as baseline. Food data were analysed using a Housing (between group) X Days (4 days) analysis of variance (ANOVA). A significant main effect for Housing was not found; indicating that the three groups of rats did not differ with respects to their daily food consumption ($F(2,21) < 1$). The Housing by Days interaction for food data ($F(6, 63) = 1.25$, $p = .29$) was also not significant. It appeared then, that prior to the Housing manipulation, the groups did not significantly differ on the measure essential to the present study.

Housing Manipulation. To assess whether moving rats from individual-housing to pair-housing affected food consumption, a Housing X Days ANOVA was used to analyse the food consumed during the eight days that the IP group rats were housed in pairs. Figure 1 shows that the IP animals' mean food consumption was significantly lower than that of animals in the other two groups immediately following the change in housing, gradually returning to control levels over a few days. Main effects for Housing ($F(2, 21) = 4.15$, $p < .05$) and Days ($F(7, 147) = 8.06$, $p < .001$), and the

Figure Caption

Figure 1: Mean food consumption (±SEM) per pair, for the three Housing conditions (IND, PAIR, IP), on each of the eight days that the rats in the IP group were housed in pairs.


70
65
60
55
50
45
40
35
0
Food Per Pair (g)
IND
PAIR
IP
1 2 3 4 5 6 7 8
Days

Housing by Days interaction ($F_{(14, 147)} = 7.87, p < .001$) were all significant. Note: In all repeated measures analyses if results are significant, they are also significant using the Greenhouse-Geiser correction.

To clarify where the groups differed, a series of one-way ANOVAs were run on each day's food data. Since it was expected that food consumption of the rats in the IP group would differ from rats in the IND and PAIR conditions, the ANOVAs were followed by two planned comparisons (IND vs PAIR and IND + PAIR vs IP). At no point over these eight days did the IND and PAIR groups show a significant difference in their food consumption (largest $F = 1.5$, $ps > .2$). However, the average consumption of the IND and PAIR groups differed significantly from the mean food intake of the IP rats on Day 1 ($F(1, 21) = 60.48, p < .001$), Day 2 ($F(1, 21) = 9.60, p < .01$), Day 3 ($F(1, 21) = 7.86, p < .05$), and Day 8 ($F(1, 21) = 4.62, p < .05$) of pair-housing the IP group. On each of these days, the IP group consumed significantly less food than the IND and PAIR groups. These results suggest that shifting rats from individual- to pair-housing suppresses food intake.

As discussed in the introduction, to support the argument that both animals were causing the food suppression in the IP pairs, the variance in body weight changes was examined. A comparison of the variance in the IP groups' change in body weight, on the first day of pair-housing, with the average variance in rats' changes in body weights across the three Housing conditions was not significant ($F_{(15, 45)} = 1.89, p > .05$). Because there was not an unusually large variance in the body weight changes amongst the IP pairs, which would be expected if only one animal within each pair was responsible for the food suppression, the results of the analysis on the food data are unlikely to be confounded by the dominance of one animal over the other.

An analysis of co-variance of the first days food data determined if the food suppression, evident in the IP pairs, was due to changes in food consumption for a single animal. When the weight change differences were co-varied out, the feeding differences between the groups, as previously found, were still evident. A main effect of Housing ($F_{(2, 20)} = 28.09$, $p < .001$) and the planned comparisons showed that the IP group (Adjusted $M = 48.22$) consumed less food than the average consumption of the IND and PAIR groups ($F_{(1, 20)} = 56.17$, $p < .001$). The IND (Adjusted $M = 62.01$) and PAIR (Adjusted $M = 62.78$) groups did not differ significantly from each other ($F_{(1, 20)} = .13$, $p > .7$).

Discussion

From the baseline data, it is evident that chronically pair-housed animals do not differ from chronically individually-housed animals, with regards to feeding. The problems that have been suggested to exist in previous studies, due to overcrowding (e.g., Fiala et al., 1977; Shelley, 1965), were not a problem in this study. Thus, the baseline data suggests that chronic pair-housing has neither a suppressive nor facilitating effect on feeding.

With a shift from individual-housing to pair-housing, a significant suppression in feeding was observed. This suggests that the effect on feeding of moving individually-housed animals to pair-housing is somewhat similar to the effect on feeding of introducing a running wheel, as feeding is suppressed in both situations.

Research looking at pair-housing, rather than group-housing, is limited; however, the results of the present study are consistent with the findings and inference made, regarding feeding, by Hoyenga and Aeschleman (1969), in their study where two rats were moved into pair-housing. They inferred, from alternate day measures of the rats' body weights, that feeding was temporarily suppressed when the animals were moved into pair-housing.

Experiment 2

In Experiment 1, it was found that moving animals from individual- to pair-housing was followed by a temporary suppression in feeding. To further explore the similarities between a shift to pair-housing and the availability of a wheel, the effects of an alternate day change in housing was explored in this experiment. Mueller et al. (in press) found that alternate day wheel access resulted in a longer suppression of feeding. For the 32 days of the experiment, (for 16 of which the alternate day wheel access group had wheels available), daily food consumption consistently decreased when wheels were available and returned to home-cage levels when the wheels were unavailable. In the present study, the effect on feeding of alternate day pair-housing was explored. Half of the control animals from Experiment 1 (chronically individually-housed and chronically pair-housed animals) were moved between individual- and pair-housing on alternate days.

The reason for the feeding suppression seen in the first experiment is not clear. As proposed earlier, the change in feeding might be attributed to an effect of novelty, or there could be something distinct about adding a reinforcer. Because, in this experiment, a group of rats will be moved from chronic pair-housing to alternate day individual-housing, it will be possible to explore the effect of novelty (the first move from pair-housing to individual-housing) in a situation with no added reinforcer. If the suppression of feeding is caused by the novelty of the new situation then it will be expected that any change in housing, whether a shift from individual- to pair-housing or from pair- to individual-housing, will be followed by a feeding suppression. However, if there is something distinct about the change to a more enriched environment (more reinforcers) then a change in rats' feeding behaviour will be expected only when there is a shift from individual- to pair-housing.

Method

Subjects. The 16 rats in the IND group and the 16 rats in the PAIR group, from Experiment 1, were maintained as in the first experiment. They were housed in polycarbonate shoe-box cages with ad-lib access to food and water.

Procedure. Following 50 days of either individual- or pair-housing, on Day 1 of this experiment four pairs were randomly selected from each of the two conditions (IND and PAIR) and moved between individual- and pair-housing on alternate days for a period of 14 days. The individually-housed rats and the previously pair-housed rats that moved between individual- and pair-housing on alternate days (groups IND-ALT and PAIR-ALT, respectively) used one set of cages for the individual-housing days and a different set for the pair-housing days. This was done so that initially the cages for pair-housing were new to both animals. Subsequently, each animal returned to the same cage/pair following each move.

Food and water intake and body weights were measured daily. Water bottles were refreshed daily and food was topped up to make approximately 160 grams of pellets available per cage. Cages and water bottles were cleaned weekly.

Results

Baseline. The daily consumption for the animals in each of the four conditions, (IND, IND-ALT, PAIR, PAIR-ALT), were analysed to ensure that there were no group differences prior to the start of the experiment. A three way repeated measures ANOVA: Housing (individual vs pair) X Change (continued vs alternate) X Days (4 days) was run on the food data.

Rats in each of the four conditions did not differ significantly with respect to daily food intake. This is evident as the main effects for Housing and Change (both $Fs_{(1, 12)} < 1$) were not found to be significant, nor were the interactions involving these factors found to be significant (all $ps > .3$). .

Alternate Day Individual- to Pair-Housing. Figure 2 shows the food data collected, on every second day, for the seven days that the rats in the IND-ALT and PAIR-ALT groups were housed in the, for them, novel conditions (IND-ALT rats pair-housed and PAIR-ALT rats individually-housed). Figure 3 shows the data collected on the alternate days, while all animals were in their original conditions. As evident in Figures 2 and 3, the only time there was a difference in the feeding behaviours between the groups was when the rats in the IND-ALT group were moved to pair-housing.

A Housing X Change X Days ANOVA of the seven days of food data collected for each 24-hour period the rats in the IND-ALT group were pair-housed and the rats

Figure Caption

Figure 2: Mean food consumption ($\pm$SEM) per pair, for the two control groups (IND and PAIR) and the two groups of rats that were moved on alternate days (IND-ALT and PAIR-ALT). Lines represent the food data collected on the seven (odd) days that the rats in the IND-ALT group were housed in pairs and the rats in the PAIR-ALT group were housed individually.

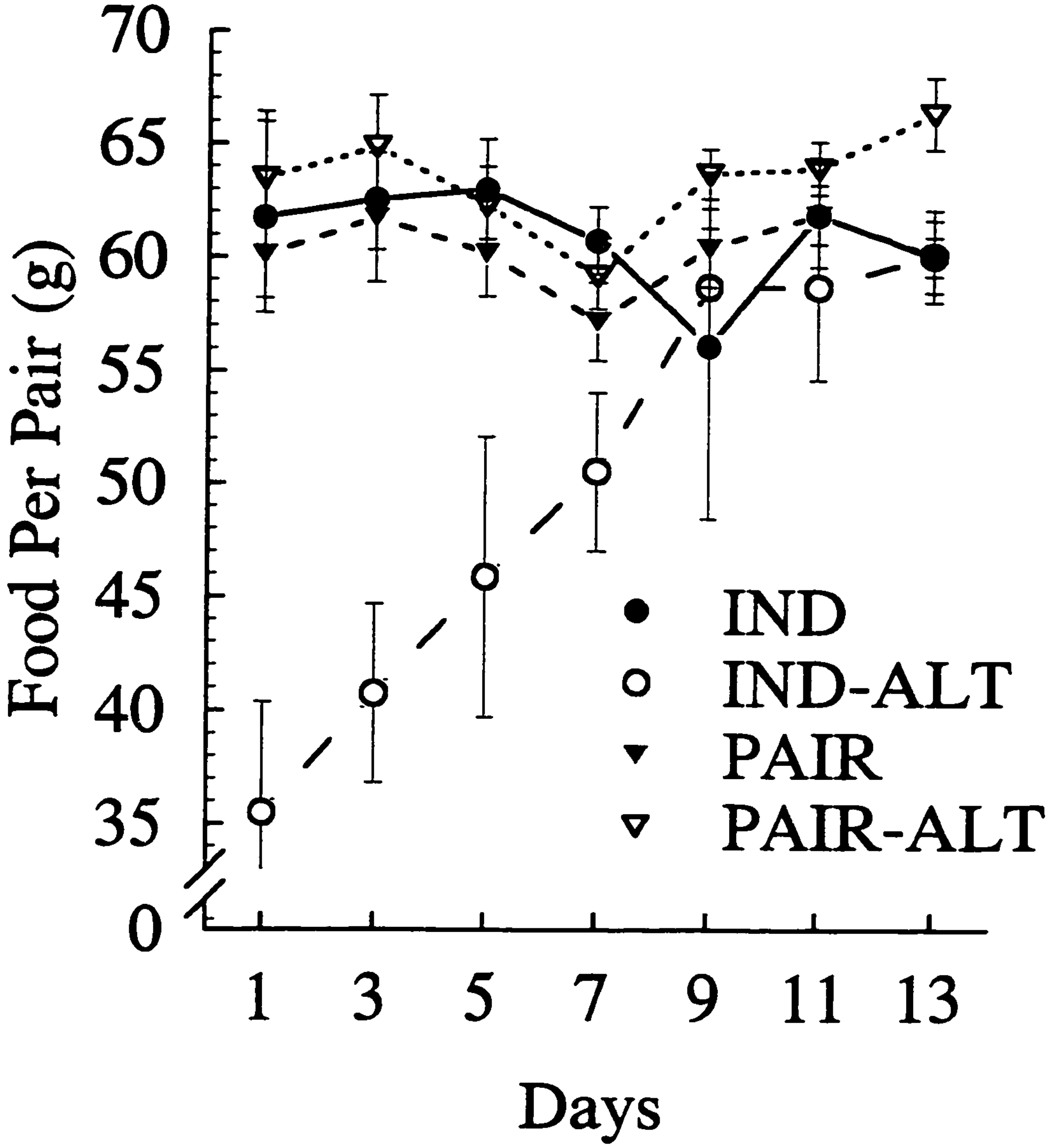
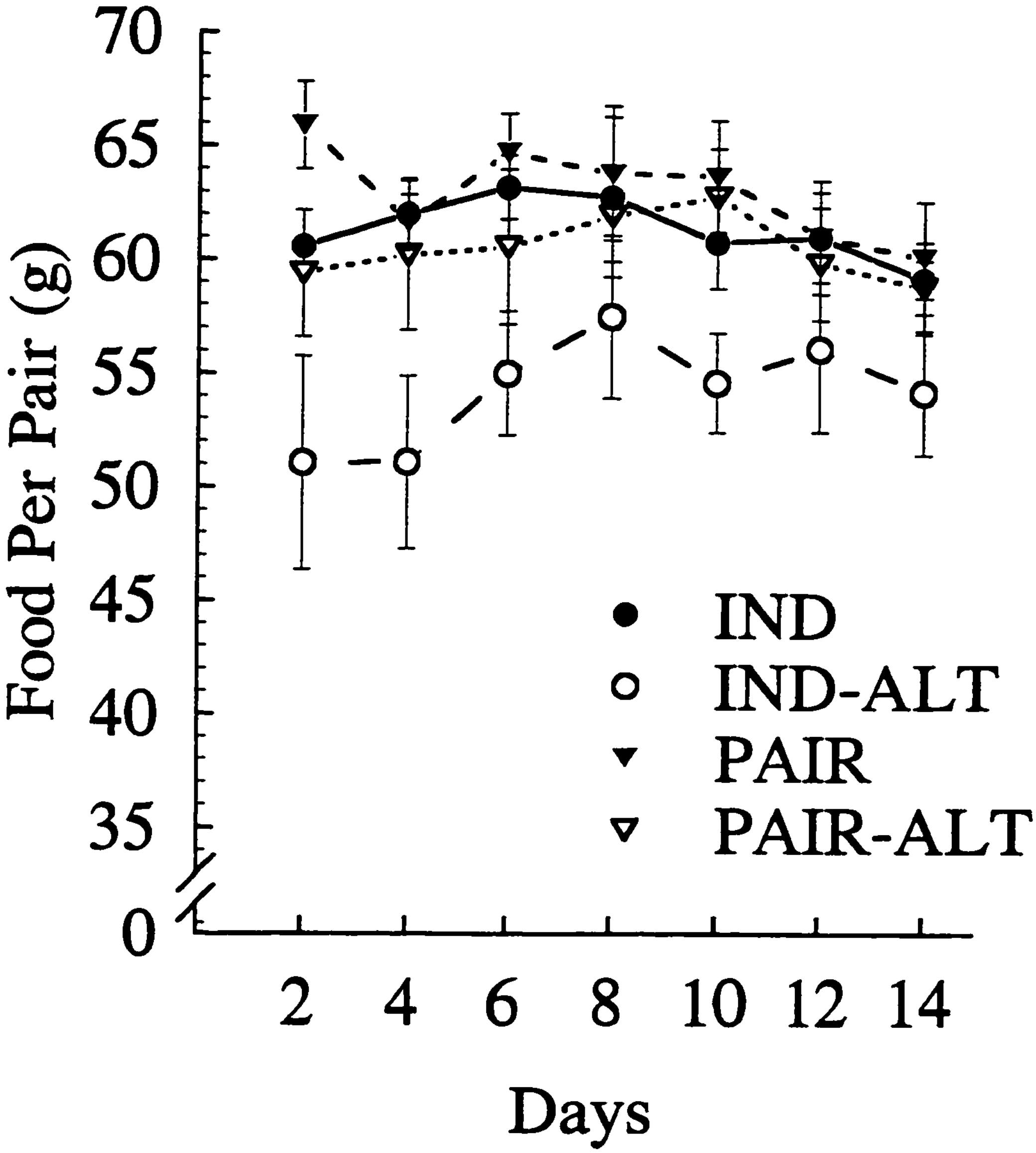

70
65
60
55
50
45
40
35
0
Food Per Pair (g)
1
3
5
7
9
11
13
Days
IND
IND-ALT
PAIR
PAIR-ALT

Figure Caption

Figure 3: Mean food consumption (±SEM) per pair, for the two control groups (IND and PAIR) and the two groups of rats that were moved on alternate days (IND-ALT and PAIR-ALT). Lines represent the food data collected on the seven (even) days that the rats in the IND-ALT group were housed individually and the rats in the PAIR-ALT group were housed in pairs.


70
65
60
55
50
45
40
35
0
Food Per Pair (g)
2
4
6
8
10
12
14
Days
IND
IND-ALT
PAIR
PAIR-ALT

in the PAIR-ALT group were individually-housed shows that a shift from individual-housing to pair-housing, following chronic individual-housing, does suppress feeding. It is evident from Figure 2 that a change from chronic pair-housing to individual-housing does not have the same suppressant effect on feeding. Only the main effects for Housing ($F(1, 12) = 8.49$, $p < .05$) and Days ($F(6, 72) = 4.46$, $p < .01$) were significant. All three two-way interactions were significant: Housing by Days ($F(6, 72) = 3.59$, $p < .01$); Change by Days ($F(6, 72) = 6.42$, $p < .001$); Housing by Change ($F(1, 12) = 10.28$, $p < .01$), as was the three-way interaction: Housing by Change by Days ($F(6, 72) = 5.49$, $p < .001$). Looking at Figure 2 it appears that the IND-ALT group were responsible for the interactions. On Days 1, 3, and 5, the rats in this group consumed less food than the other three groups.

When all animals were in their original conditions, the 2 (Housing) by 2 (Change) by 7 (Days) ANOVA on food consumption revealed only a significant Days effect ($F(6, 72) = 3.25$, $p < .01$). The main effects for Housing ($F(1, 12) = 2.93$, p = .11) and Change ($F(1, 12) = 4.37$, p = .06), and all the interactions involving these factors (all $ps > .06$), were not significant (Housing X Change: $F(1, 12) = 1.02$, $p = .33$).

Because only the IND-ALT group shows a suppression in feeding when pair-housed, it was necessary to consider the possibility that one rat in the pair was responsible for the feeding pattern for this group. Comparing the variance in the weight changes for the rats in the IND-ALT condition to the average variance for all rats, it appears that the effect on feeding observed when the IND-ALT rats were moved to pair-housing is not the equal result of each animal in the pair. The variance in the weight changes for the rats in the IND-ALT group is significantly different from the average variance ($F_{(7, 28)} = 3.34, p < .05$), such that the standard deviation is much larger for this group (*SD* = 15.05) than for the IND (*SD* = 4.52), PAIR (*SD* = 3.27), and PAIR-ALT (*SD* = 3.62) groups.

Despite the difference in variances, the individual- to pair-housing effect is still evident when the difference in weight change for animals in each pair on the first day of experimental manipulation is co-varied out. The analysis of co-variance revealed only a significant interaction of Housing by Change ($F_{(1, 11)} = 5.78, p < .05$). The source of the interaction is understood by looking at the simple main effects of Change at both levels of Housing. The means indicate that the IND-ALT grouped rats consumed significantly less food (Adjusted *M* = 42.30) than the IND grouped rats (Adjusted *M* = 60.20) on Day 1 ($F_{(1, 11)} = 6.73, p < .05$). However, the rats in the PAIR (Adjusted *M* = 57.74) and PAIR-ALT (Adjusted *M* = 60.55) groups do not significantly differ ($F_{(1, 11)} = .34, p = .57$).

Discussion

In Experiment 2, where one group of rats was shifted from chronic individual-housing to pair-housing on alternate days, a suppression of feeding was observed on the pair-housing days and there was a return to control levels on the days that they were individually-housed. This is similar to the alternate day wheel access study such that on the days where there was wheel access, daily food intake decreased significantly, and returned to homecage levels on the alternate days, when wheels were unavailable.

However, unlike alternate day wheel access where rats continue to decrease their intake on days where the wheel is available, in the present study, the IND-ALT rats only showed a suppression in feeding on the first three days of pair-housing.

The decrease in feeding in this experiment is much greater than the initial decrease seen in the first experiment when rats were moved from individual- to pair-housing. The duration of individual housing, prior to the move to pair-housing, and the age of the animals may be the source of the difference. Looking at the variance of the weight changes on the first day, the rats in the IND-ALT group show a significantly different/larger weight change variance in comparison to the average variance of all 32 animals in this experiment. This variance difference is not found between the rats in the IND, PAIR, and IP groups in the first experiment. This suggests that some additional effect occurred here; the actual change in feeding (percentage) can not be accurately compared between the two studies. However, since there was still a group difference following the analysis of co-variance (co-varying out weight difference between pairs) in Experiment 2, the main finding that there is a temporary effect on feeding seems accurate.

The results of this study also suggest that an effect of simple novelty is not an adequate explanation for the suppression in feeding. If the suppression in feeding was a result of simple novelty then moving chronically pair-housed rats to individual-housing on alternate days would have resulted in a significant decrease in their feeding, at least on the first 24-hour period of individual-housing. However, rats in the PAIR-ALT group were similar on individually housed days to rats in the IND and PAIR groups (see Figure 2). The distinct difference between the novelty of moving to pair-housing compared to moving rats into individual-housing may be the effect of stress, such that the addition of another rat is stressful. This theory coincides with the results of a study conducted by Brown and Grunberg (1996), where there was evidence of stress when animals were moved into group-housing. Stress may explain the severe suppression in feeding shown in this experiment, where the animals are older and have been individually-housed for a much longer period, compared to the rats in the IP group in the first experiment.

Experiment 3

As previously discussed, Premack and Premack (1963) suggest that reinforcers are interchangeable and the time spent working for a particular reinforcer depends on what else is available. With fewer reinforcers available, more time will be spent on each in comparison to a situation where time allocated to reinforcers must be divided between several reinforcers. In finding that moving animals from individual-housing into pair-housing does result in a decrease in feeding, the next step was to explore the effect of adding two reinforcers simultaneously.

The majority of studies that have considered the interaction between wheel running and feeding in rats, have only looked at animals housed individually (Bauman, 1992; Collier, 1970; Jennings & McCutcheon, 1974; Levitsky, 1970; Looy & Eikelboom, 1989; Premack & Premack, 1963; Tokuyama et al., 1982). Only Goodrick, Ingram, Reynolds, Freeman, and Cider (1983) have had a condition where two animals were given access to a wheel, but they were mainly concerned with the lifespan of rats housed in activity cages and given either ad lib or alternate day access to food, so only the long-term weight changes in pair housed rats given running wheel access were addressed. In Goodrick et al.'s (1983) study a group of rats housed individually with wheel access was not included, daily food consumption was not measured, and rats were only weighed once a month; therefore, day by day changes could not be assessed.

The purpose of this third experiment was to determine if the effect on feeding would differ if animals were introduced to both the wheel and pair-housing at the same time, rather than either moving rats to pair-housing or introducing running wheels. One group of animals was continually individually-housed (IND group), another remained individually-housed but was given wheel access (IND-WHEEL group), a third group was moved from individual-housing to pair-housing (IP), and a final group was simultaneously given wheel access and moved into pair-housing from individual-housing (IP-WHEEL). Due to equipment limitations, the study was run in two replications such that half of the animals in the IND, IND-WHEEL, IP, and IP-WHEEL groups were run in the first replication and the remaining animals were run in the second replication.

Method

Subjects. Forty-eight male Sprague-Dawley rats (approximately 180-215 grams) from Charles River Canada were housed in polycarbonate shoe-box cages (47.5 x 26.25 x 20 cm); like those used in Experiment 1 and 2. All animals were individually housed upon arrival to the laboratory.

Throughout the experiment, rats had ad-lib access to Rat Diet (PMI Feeds Inc.) pellets and tap water, and were handled daily. The holding room was maintained on a 12:12 light-dark cycle (lights on between 7:00 am and 7:00 pm) and kept at a temperature of approximately 21^{0}C.

Apparatus. In addition to the polycarbonate shoe-box cages, six individual hanging wire cages (25 x 17.5 x 20.5 cm), two wire cages (25 x 40 x 18 cm), each with one running wheel (11 cm wide, 33 cm diameter) attached, and one wire cage (25 x 64 x 18 cm), with one running wheel attached, were utilized.

Wheel turns were recorded in 5 second bins using a Mini-Mitter Co. data collection system run on a Zenith 151 computer using version 2.3 of the Dataquest III software.

Procedure. Upon arrival, all rats were randomly assigned to pairs for the purpose of data collection and later housing changes. For the first four days, the rats were only handled on a daily basis. Body weights were measured from the fifth day following their arrival (Day -17 of the experiment). Food and water consumption were collected daily throughout the experiment starting on Day -8. On Day 0 (22 days after arrival), six rats were moved into the wheel equipped hanging wire individual cages (IND-WHEEL group), six rats were pair-housed and moved into the wheel equipped hanging wire gang cages (IP-WHEEL group), six rats were moved into pair-housing (IP group), and six rats (IND group) remained individually housed. The rats were housed in their respective conditions from Day 1 to Day 8, at which time they were returned to individual-housing. On Day 8 the remaining animals in the four groups were moved into their respective wheel/housing conditions. On Day 16 these animals were returned to individual-housing. Wheel running was recorded continuously.

Results

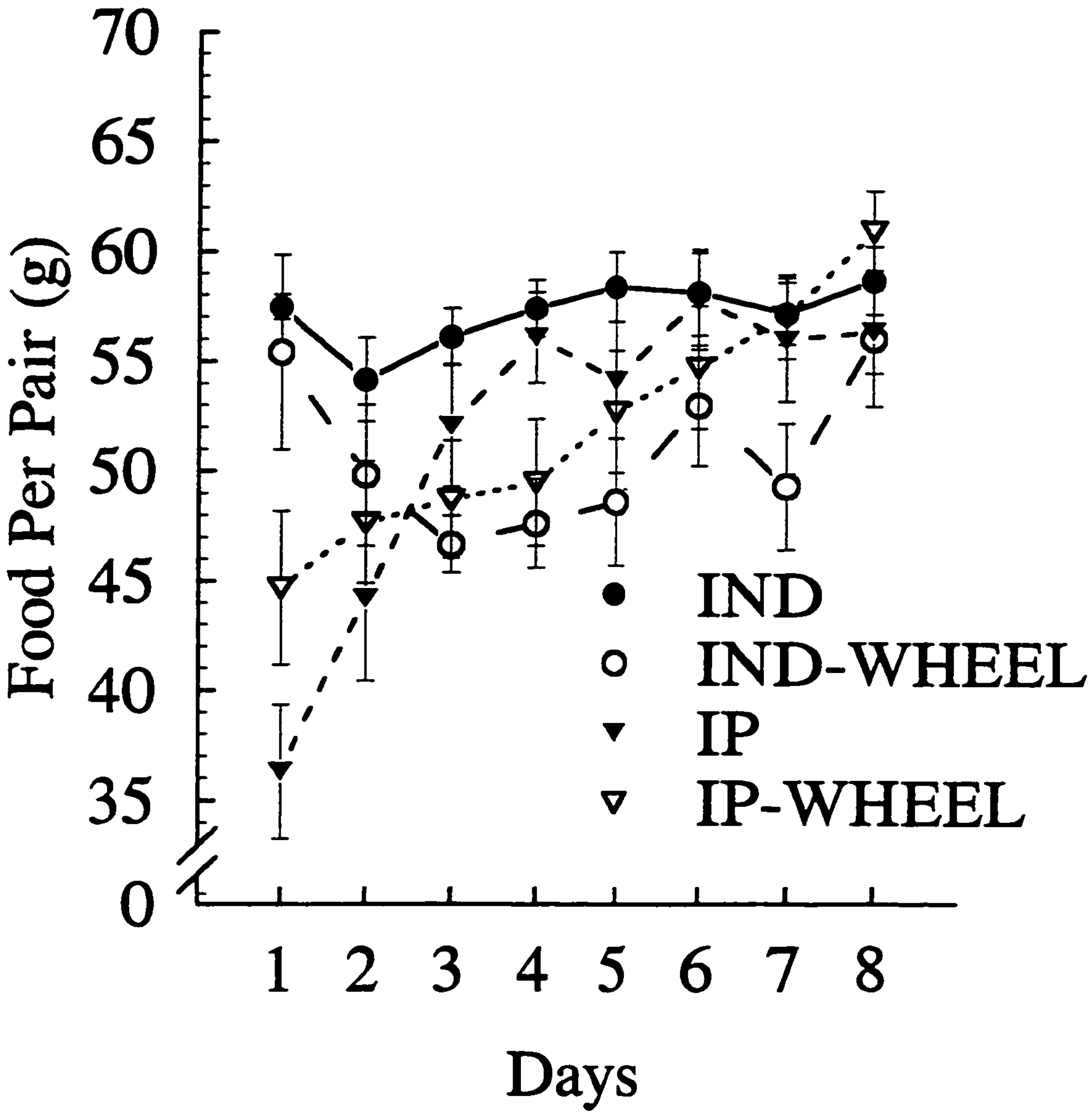
Baseline. To ensure that the rats in each group did not differ with respects to food intake before the experimental manipulation, four days of data, prior to each replication, were analysed. A four-way repeated measures ANOVA: Housing (individual vs pair) X Wheel (wheel access vs no wheel access) X Session (replication 1 vs replication 2) X Days (4 days) was run on the food data.

Feeding was not found to differ based on the Housing and Wheel condition that rats were assigned to. This was evident as the main effects for Housing and Wheel (both $Fs_{(1, 16)} < 1$) and all interactions involving these factors were not significant (all $ps > .3$). However, there was a significant difference based on Session as the analysis of the food data revealed a Session X Days interaction ($F_{(3, 48)} = 11.66$, $p < .001$). This difference in feeding based on Session is not surprising as the baseline data collected for the rats in Session 2 was eight days later than the baseline data for the first group of rats.

Pair-Housing and Wheel Access. Figure 4 shows the food data collected on the eight experimental days (combined Session 1 and 2 data). A Housing X Wheel X Session X Days ANOVA on food data collected during the experimental sessions revealed only a significant Days effect ($F_{(7, 112)} = 15.93$, $p < .001$), a Housing by Days interaction ($F_{(7, 112)} = 13.33$, $p < .001$), and a Wheel by Days interaction ($F_{(7, 112)} = 5.38$, $p < .001$). Because the interactions involving the Housing X Wheel

Figure Caption

Figure 4: Mean food consumption ($\pm$SEM) per pair, for the two control groups (IND and IP) and the two groups of rats that were moved into wheel equipped cages (IND-WHEEL and IP-WHEEL). Lines represent the food data averaged across Session.


70
65
60
55
50
45
40
35
0
Food Per Pair (g)
IND
IND-WHEEL
IP
IP-WHEEL
1 2 3 4 5 6 7 8
Days

conditions were not significant, it is appropriate to analyse the Housing X Days and Wheel X Days interactions separately.

Figures 5 and 6 show the same food data as Figure 4 but averaged across the Wheel and Housing conditions, respectively. It is evident from these graphs that there was an immediate effect on feeding of animals being moved from individual- to pair-housing, and a delayed effect on feeding of the introduction of a wheel. A series of one-way ANOVAs show that the animals moved into pair-housing (IP and IP-WHEEL groups) consumed significantly less food than the individually-housed animals (IND and IND-WHEEL groups) on the first day of manipulation ($F(1, 22) = 22.99$, $p < .001$). Also, the between group difference approached significance on the second day ($F(1, 22) = 4.14$, $p = .054$), again, showing that pair-housed animals consumed less than the individually-housed animals. In comparing the food data based on the Wheel conditions, it is evident that the animals moved into the cages equipped with wheels (IND-WHEEL and IP-WHEEL groups) temporarily consumed less food than the rats without wheel access (IND and IP groups). The suppression in feeding was evident on the third ($F(1, 22) = 8.89$, $p < .01$), fourth ($F(1, 22) = 15.74$, $p < .001$), and fifth day ($F(1, 22) = 4.69$, $p < .05$).

Figure 7 shows the average daily running per pair over the eight days of wheel availability. It appears that moving rats from individual- to pair-housing does not have an effect on daily running. A Housing X Session X Days ANOVA revealed only a significant Days effect ($F(7, 56) = 39.97$, $p < .001$).

Figure Caption

Figure 5: Mean food consumption ($\pm$SEM) per pair, for each of the two Housing conditions (Individually Housed and Moved to Pair Housing). Lines represent the food data averaged across the Wheel condition and Session.

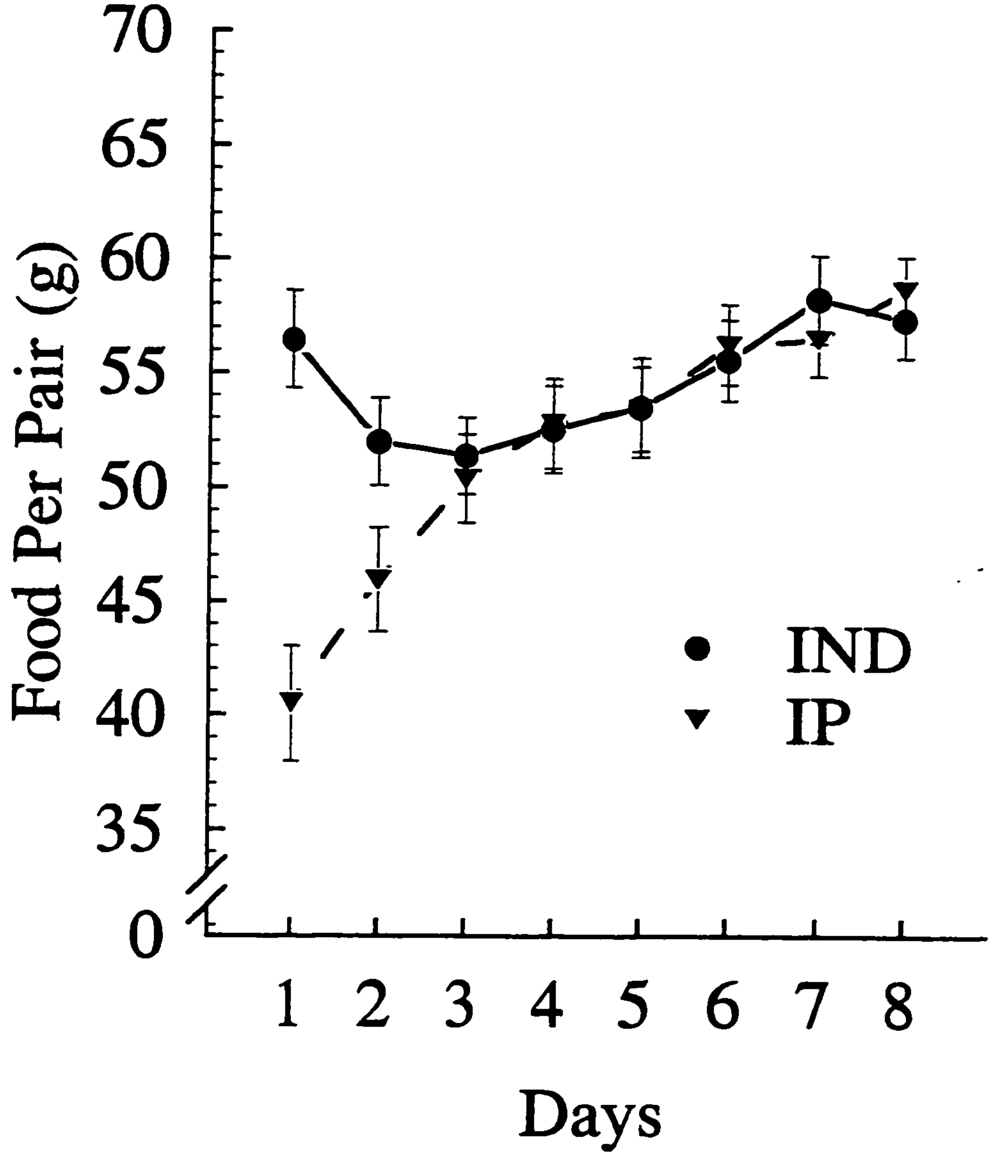

70
65
60
55
50
45
40
35
0
Food Per Pair (g)
IND
IP
1
2
3
4
5
6
7
8
Days

Figure Caption

Figure 6: Mean food consumption ($\pm$SEM) per pair, for each of the two Wheel conditions (Wheel and No Wheel). Lines represent the food data averaged across the Housing condition and Session.

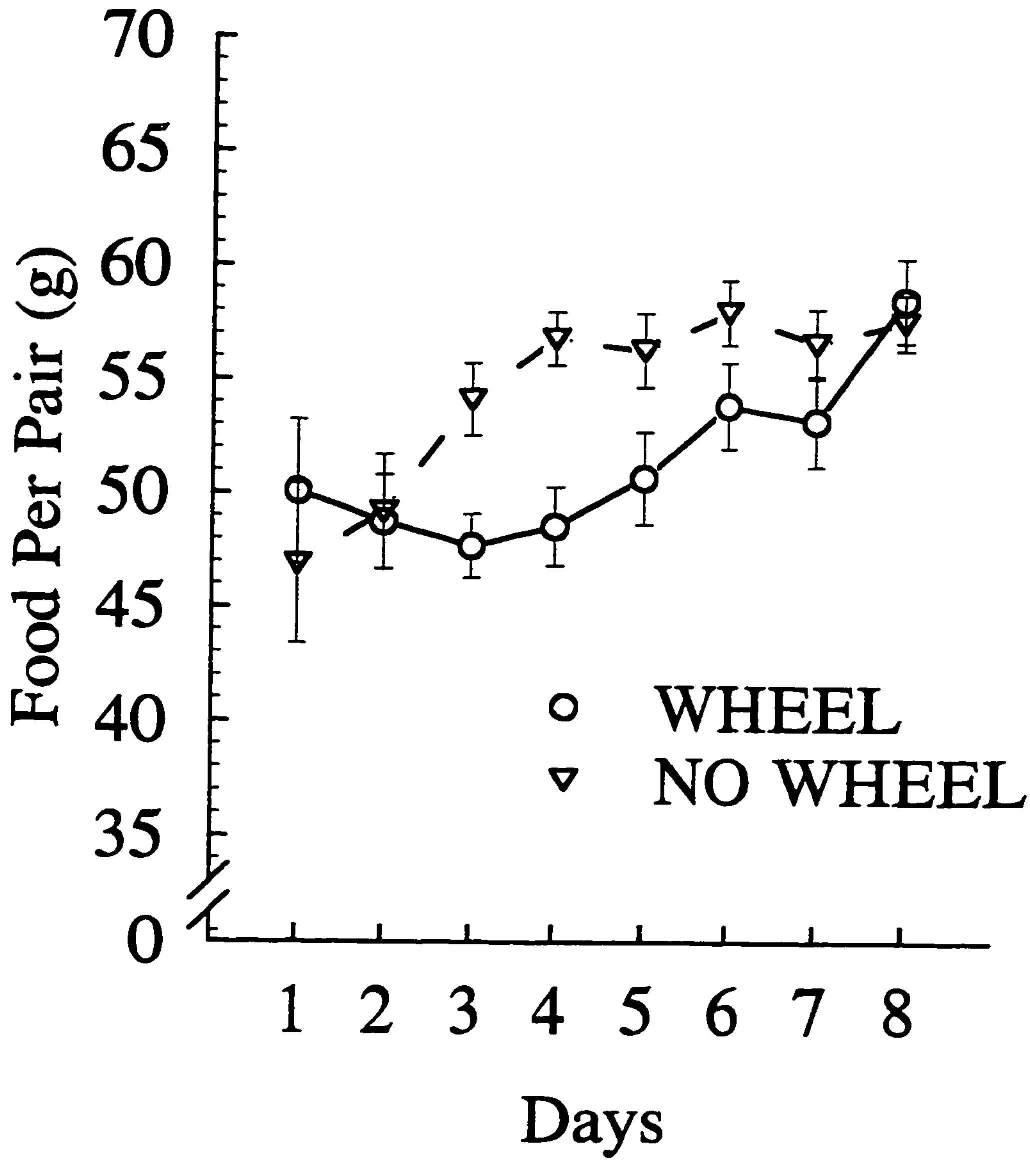
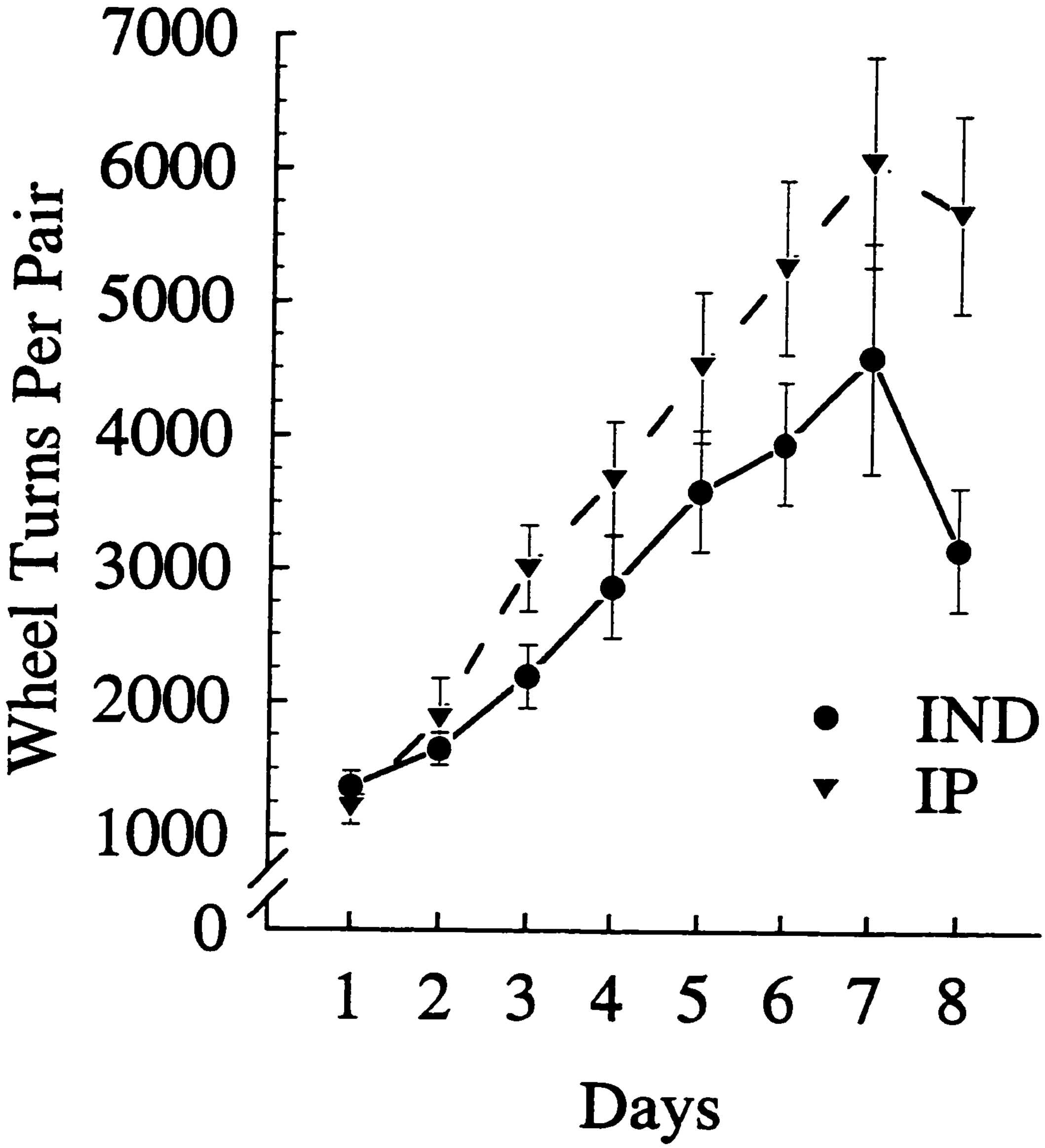

70
65
60
55
50
45
40
35
0
Food Per Pair (g)
WHEEL
NO WHEEL
1
2
3
4
5
6
7
8
Days

Figure Caption

Figure 7: Mean number of wheel turns per 24 hours ($\pm$SEM). Lines represent the average number of wheel turns per pair for animals housed individually and for those moved to pair-housing.



7000
6000
5000
4000
3000
2000
1000
0
Wheel Turns Per Pair
1
2
3
4
5
6
7
8
Days
IND
IP

Discussion

As in the first experiment, there was a temporary decrease in feeding when individually-housed rats were moved to pair-housing, and consistent with wheel running studies there was a temporary suppression in feeding when individually-housed animals were moved into wheel equipped cages. Unique to the present study was the food data of rats that were simultaneously pair-housed and given running wheel access. The analyses of the food data indicated that pair-housing rats in wheel equipped cages did not appear to have an additive effect on feeding. Rather, it appeared that pair-housing had an immediate and short-term effect on feeding. This lasted for such a brief period of time that by the third day, when the wheel was showing an effect on feeding, the pair-housing effect had disappeared.

Somewhat surprisingly, in view of the hypothesis that the more reinforcers available, the less time spent with each, the rats in the IP-WHEEL group ran just as much as the rats in the IND-WHEEL group. However, it is important to note that the effect on feeding of pair-housing rats seems to have disappeared by the time the wheels became salient (running was high and feeding was suppressed); therefore, the reinforcing value of pair-housing may have not lasted long enough to have an impact on wheel running.

General Discussion

The suppression in feeding observed when rats have access to running wheels is not replicated by just any enrichment to the environment. In the present series of studies, where rats' environment was enriched by a change in housing (moving rats from individual- to pair-housing), the changes in rats' feeding were different from that shown when rats have access to wheels. Although there was a temporary suppression in feeding when rats were moved into pair-housing from chronic individual-housing, the pattern of this suppression appears to be distinct from that observed in wheel running studies. This difference is evident when a comparison is made between the first experiment presented here and studies where rats have chronic wheel access (Bauman, 1992; Collier, 1970; Jennings & McCutcheon, 1974; Levitsky, 1970; Looy & Eikelboom, 1989; Premack & Premack, 1963; Tokuyama et al., 1982). Secondly, the effect on feeding of alternate day pair-housing is temporary when compared to the effect of alternate day wheel access on feeding (Mueller et al., in press). Finally, in the third study, the effect of simultaneously moving animals into wheel equipped cages and into pair-housing clearly demonstrated the different effects on feeding.

In all three studies a temporary decrease in feeding is shown following the move of animals from individual-housing to pair-housing. However, the temporal pattern of the suppression in feeding following this housing shift seems to be different from that shown in wheel running studies. It was found that when rats were moved from individual- to pair-housing, in all three studies, the effect on feeding was immediate, within the first 24 hour period. With wheel access, as evident in Looy and Eikelboom (1989), and the third study, the decrease in feeding was not maximum until after a few days of wheel access. The return to baseline feeding was also much faster for the animals that were moved from individual-housing to pair-housing compared to those that had wheel access. With long term chronic wheel access, feeding behaviours typically recovered to home-cage levels within about seven to ten days (e.g., Levitsky, 1970; Looy & Eikelboom, 1989; Tokuyama et al., 1982); whereas, in the first and subsequent experiment rats that were moved from individual- to pair-housing were found to recover their feeding by the fourth day of pair-housing. The differences in the time period is particularly evident in the third experiment. Feeding was affected immediately by the change in housing (individual- to pair-housing) but the effect was so brief that by the time the effect on feeding of wheel access became evident, there was no longer a housing effect.

It is important to note that the different effects on feeding of moving rats to pair-housing compared to wheel introduction, is not attributable to intensity differences. If the duration difference was a result of the intensity of the reinforcer then it would be expected that with the greater the intensity, the decrease in feeding would be larger and last longer. However, when the initial decrease in feeding of the rats that were moved from individual-housing into pair-housing in Experiment 1 and Experiment 2 are compared, a large difference in the percentage of decrease is evident, but the duration of the effect remains constant. In Experiment 1 there was a 23% decrease in the rats' feeding when they were moved from individual- to pair-housing; whereas, in Experiment 2, rats moved into pair-housing showed a 40% decrease in their feeding. In both studies rats' feeding recovered to control levels by the fourth day. In wheel running studies, for example Looy and Eikelboom (1989), feeding decreased by 37% with the introduction of the wheel (a level greater than that shown in Experiment 1 but similar to that in Experiment 2), but recovery took seven to ten days. This suggests that temporal differences are not just due to intensity of the effects.

Several aspects of the present series of studies and the findings of a recent study by Brown and Grunberg (1996), indicate that the addition of another animal, following a period of individual-housing, may result in suppressed feeding due to the stress associated with the novelty of the situation. Brown and Grunberg (1996) found that in moving rats from individual-housing to a crowding situation (10 rats per cage) corticosterone levels were much higher in the animals that had been crowded for 18 hours compared to those that remained individually-housed. This suggests that these animals were highly stressed.

In Experiment 2, with the alternate day change in the animals' housing, it is apparent that an effect of novelty/stress should be considered. Animals that were originally individually-housed and were then moved to pair-housing on alternate days, like those moved to chronic pair-housing in the first experiment, showed suppressed feeding on the first three days of pair-housing. Novelty/stress seems to be the key issue here as the number of presentations of pair-housing affected feeding similarly whether or not there were intervening days to "catch up" on their feeding. In Mueller et al.'s (in press) alternate day wheel access study rats suppressed their feeding each time the wheel was reintroduced; the suppression in feeding lasted for the duration of the study. The present experiments suggest that this wheel effect is not due to novelty/stress.

Also, the present studies show that simple novelty is not sufficient to suppress feeding as a move from pair-housing to individual-housing, in Experiment 2, does not suppress feeding rather, suppressed feeding occurs only following a move from chronic individual-housing to pair-housing. Moving to pair-housing seems more stressful than moving to individual-housing. Stress appears to be a component of the suppression resulting from the move to pair-housing as when the effect on feeding of initially moving animals from individual- to pair-housing in the first and last study are compared with the effect in the alternate day experiment, the intensity of the effect is different. The rats in Experiment 2, who had a longer period of individual-housing prior to the shift showed a greater suppression in feeding. It is possible that age and period of individual-housing prior to the shift may have played a role, making the change more salient.

Initially three theories were proposed for the cause of suppressed feeding following the introduction of running wheels. An effect specific to the wheel (activity), novelty of the wheel, and the number of available reinforcers were all suggested as theories for the source of the suppression in feeding. In the present series of studies, the shift from individual-housing to pair-housing was used to explore these explanations. Novelty/stress appears to account for the feeding suppression evident following a move to pair-housing. However, because of the different temporal pattern, onset, and duration of the suppression following wheel introduction, compared to moving animals to pair-housing, novelty/stress does not adequately explain why rats show suppressed feeding when wheels are available. The explanation based on the number of reinforcers also does not seem to adequately account for feeding suppression with wheel access. If the increase in the number of available reinforcers was the source of the suppression, then differences in feeding and/or wheel running would be expected between the group of rats that were both moved to pair-housing and given wheel access compared with rats that were just moved to pair-housing or just moved to wheel equipped cages. This did not happen. Because the temporal pattern of the suppressed feeding was so different when animals were moved to pair-housing compared to when wheels were made available, at this point it can not be ruled out that there is a specific activity effect on feeding.

The present series of studies found that a change in rats' housing, when it involves a move from individual-housing to pair-housing, results in a temporary suppression of feeding. Interestingly, the duration of the suppression remained consistent across all three experiments. Increasing the period of individual-housing (from Experiment 1 to 2), prior to the shift to pair-housing, changed the degree of feeding suppression, but the duration of the suppression remained at three days. Rats' feeding behaviours returned to control levels by three days of pair-housing even when the rats were returned to individual-housing on intervening days. These studies suggest that novelty/stress causes rats' feeding suppression following the change from individual- to pair-housing. By comparing these findings to those of wheel running studies, it is possible to exclude novelty/stress as the cause of the wheel induced feeding suppression.

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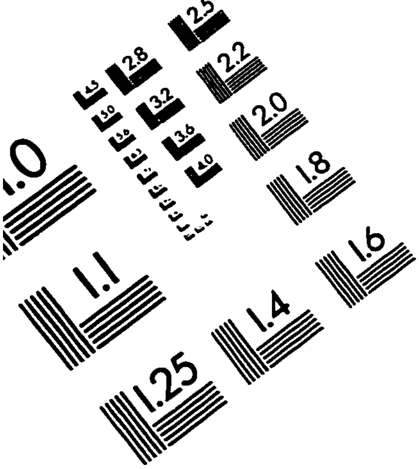

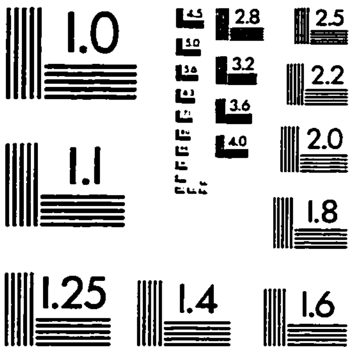

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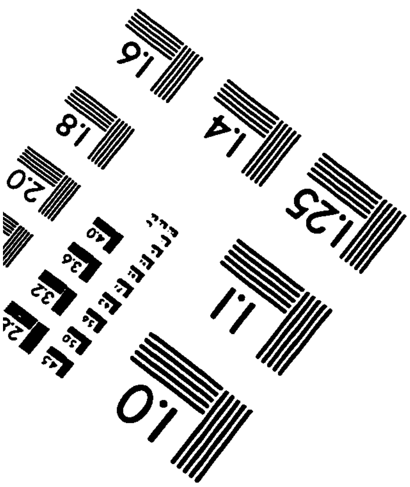

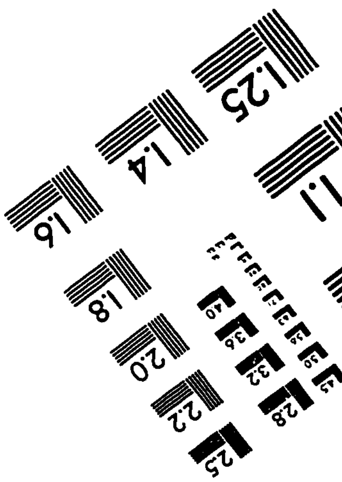

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